The Efficiency of a Seine Net

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Abstract.—We present a method to predict the capture efficiency of a 25-m, 5-mm mesh seine net as a function of fish size and taxon from a diverse fish community. This allows true abundance and size distribution to be estimated from observed catches. Predicted capture efficiency from an empirical model of field calibrations from the Amazon River floodplain was a positively skewed, unimodal function of fish length, whose magnitude depended on method of seine operation and fish taxonomic group. Capture efficiency is the product of efficiency of encirclement as the net is laid (which decreases with increasing fish size) and efficiency of retention as the net is hauled (which increases with increasing fish size). Retention was determined by modeling mark–recapture data. Dividing observed capture efficiency by this retention yielded empirical encirclement efficiency, which was then compared with encirclement efficiency determined from a simulation model of fishes' evasive behavior. The simulation accounts for the fishes' swimming speed relative to the speed of deployment of the seine, threshold distance (how close the disturbance from laying the net must be to initiate evasion), appraisal time (how long a fish continues evasive behavior when it moves outside the threshold distance), and the directionality of evasive movements. Simulated results of encirclement efficiency corresponded to empirically based predictions within plausible ranges of the simulation variables above, although for fish of length exceeding about 50 cm there is a high coefficient of variation in captured biomass due to small numbers and low catchability. We conclude that the method can be used for a wide range of conditions to convert seine capture data to unbiased estimates of abundance and size distribution, but that empirical determinations will still be needed for different net specifications and sampling conditions.

Estimating fish population numbers and size structure accurately is an elusive goal. A seine net of appropriate design is a simple, yet effective, tool for sampling in waters where its passage is not impeded by unremovable snags. Although seine nets have been used by fishers since antiquity and for more than 100 years for scientific and management purposes, most researchers still do not know what relationship exists between their catch and the actual abundance or size distribution of fish in a defined area.

Studies to estimate seine efficiency or to determine factors influencing efficiency have covered a variety of sampling methods, habitats, and assumptions (Fredin 1950; Threinen 1956; Weinstein and Davis 1980; Penczak and O'Hara 1983; Wiley and Tsai 1983; Lyons 1986; Parsley et al. 1989; Pierce et al. 1990; Allen et al. 1992; Bayley and Dowling 1993; Holland-Bartels and Dewey 1997), all of which include estimates of substantial biases and warnings about the consequences of ignoring

them. Although most reports acknowledge escapement of fish following closure, net avoidance prior to closure has received less attention (Kjelson and Colby 1976). Calibration for unbiased efficiency estimates requires that the same opportunities for escapement that occur during standard operation are provided in the experiment and that the vulnerable population can be estimated with sufficient accuracy and on an appropriate spatial scale. In addition, accounting simultaneously for taxa, fish size, and uncontrollable environmental effects is necessary to provide unbiased estimates from catch data.

These issues present a difficult challenge, especially in many temperate systems where seasonally dependent fish sizes and correlated environmental factors affecting catchability occur. Here we took advantage of an environment with a wide range of fish densities, contrasting fish taxa of overlapping size ranges, and relatively few physical variables in order to predict capture efficiency empirically and understand some of the processes through simulation. The local goals were to quantify associations of fish with habitats and

make inferences at larger scales of abundance, biomass, and production. This required a knowledge of capture efficiency so that valid local abundance estimates could be made.

Our method treats seine capture efficiency as a product of encirclement when the seine is laid and retention when it is hauled. The seine is used in conjunction with an outer block net for calibration experiments. Mark–recapture allows measurement of retention of the block net and therefore produces estimates of seine net efficiency. Dividing capture efficiency by estimated retention yields encirclement estimates, which are then compared with encirclement calculated from a simulation model of fishes' evasive behavior. Data are from 22 calibration experiments in the Amazon River floodplain that covered a wide range of species and sizes of individuals.

We first describe the sampling protocol for standard sampling and calibration experiments. This is followed by the analytical approach to empirical prediction of catchability. The biological background to the simulated process of net evasion is followed by a description of the simulation model. Results of empirical models are followed by a comparison of predicted and simulated net evasion. Finally, the discussion focuses on biological and sampling implications.

Methods

Sampling Protocol

Standard 25-m seine.—The seine net described is frequently used to sample fish in the central Amazon floodplain near Manaus, Brazil, throughout the hydrological cycle. Its effective use is recommended for water depths less than about 3.5 m and for areas where rooted vegetation or woody debris can be removed manually.

The standard seine was 25 m long when hung, the original 40 m of netting being tucked at intervals to form a series of bags. Net depth was 6 m in the middle portion, tapering to 60 cm at the ends. The netting was of braided, knotless, dark blue nylon with a stretched mesh size of 5 mm, excluding the 0.5-mm twine diameter. The lead line contained 120-g lead cylinders at 35-cm intervals. Floats, 15 cm in diameter, were spaced at 30-cm intervals.

This net was chosen because it conformed to an appropriate quadrat size for sampling fish in common floodplain habitats, because it was cost efficient for obtaining sufficient samples, and because professional fishers had demonstrated its effec-

tiveness during previous research surveys in floodplain habitats for a broad range of species and fish sizes. The floodplain environment sampled is covered by turbid or 'black' waters containing a patchy distribution of rooted-emergent or floating vegetation and abundant organic debris combined with generally smooth muddy or silty substrates (Junk 1973; Fittkau et al. 1975). Subsequently, longer nets of this mesh size were impractical because of excessive drag caused by abundant fine debris and the frequency with which samples would need to be abandoned due to snags.

All methods using this seine required a heavy, wooden 7.5-m canoe, with fishers paddling fore and aft and a third paying out the seine. When approaching and encircling the site, maximum silence was maintained, with noise being restricted to movements of the paddles, boat, and net contacting the water. Because fishing was confined to depths of less than about half the net depth, the full water column could be swept while maintaining a belly in the net. Three distinct operational methods used in daytime are described here.

Method A: A circle was described by the canoe so that 0–4 m separated the ends of the net. This encirclement took close to 40 s. Any gap was immediately closed and the lead line inspected to ensure contact with the bottom. Samples were abandoned if the lead line was found to be suspended by a snag.

Trials demonstrated that catches were unacceptably low and selective when rooted vegetation was not cleared before hauling. Therefore, following closure and lead line inspection, the enclosed area was cleared of any rooted vegetation, as well as any large detrital material and tree trunks. Four people hauled slowly; the two pulling the lead line with hands on the substrate squatted together to provide a human barrier (Figure 1A). The gathered lead and float lines were then lifted into the canoe, leaving the belly of the net with fish in the water. This method was restricted to where the minimum depth was less than 80 cm so that those pulling the lead line could breathe.

A variant of this method was used where hard, woody vegetation could hold up the lead line. An annular path for the net was cleared manually, and the area left for at least 1 h. The net was then laid, cleared of enclosed vegetation, and fished as described.

Method B: This was a beach-seining operation with a semicircular set taking close to 40 s. The lead line was checked and the enclosed area

FIGURE 1.—Calibration examples: **(A)** hauling 25-m seine using method A in open water, **(B)** 25-m seine and block net setting in vegetation (mainly *Paspalum repens*) before hauling by means of method A.

cleared as in method A. Four persons hauled the net slowly.

Method C: The net was fished as a lampara seine (Hayes 1983). It was laid in a circle leaving 8–12 m between the ends. During rapid hauling into the canoe, personnel stamped on the floor boards, as is standard practice in commercial operations, to frighten fish into the belly of the net. Samples were aban-

doned if a snag was encountered. This method was used where minimum depth exceeded 80 cm, in open waters with and without floating plants, or where rooted plants or woody debris not sufficiently dense to impede hauling.

Calibration.—The block net was designed to isolate a portion of the fish community, permit one of the standard operational methods (A, B, or C) of the 25-m seine within, and allow for fish to evade the seine while being encircled. The block net had the same mesh and median depth as the seine, but with deep ends to facilitate blocking. It was 50 m long when hung and consisted of 85 m of netting. Distance between lead weights was 50 cm and between floats, 25 cm.

The block net was laid from the canoe, marked fish were released inside, the 25-m seine was fished inside once, and finally the 50-m block net was hauled. Because efficiency was determined from the enclosed population, evasion while laying the block net was unimportant, providing that sufficient numbers spanning the fish community were enclosed. The seine was fished concentrically within the block net in methods A and C where the bottom was fairly level (Figure 1). Where the bottom sloped considerably (all method B samples and nos. 18 and 19 of method C; Appendix 1), association with depth of some species and individual sizes was anticipated, and a concentric design would result in a significant area of deeper water being included in the block net that was not swept by the seine. Therefore, a block net configuration was calculated such that each depth was sampled at a constant proportion by the seine. The block net configuration follows the equation of an ellipse (or half ellipse in the case of method B) and was marked with rods prior to fishing to guide the fishers. The nets only touch at the vertex of the minor axis at the deepest point (and at the shallowest point in the aforementioned method C calibrations), so the freedom of fish to escape encirclement is negligibly compromised (the derivation is available from P. Bayley).

Fish for mark and release (Appendix 2) were seined from surrounding, similar habitats. Marked fish were distributed among buckets that, with the aid of poles, were subsequently used to distribute the fish evenly inside the block net so that the area was not disturbed by boats or wading. Marked fish introduction began 5 min after the block net was laid, was completed in 5–10 min, and was immediately followed by the 25-m seining operation. The block net, which was laid in a similar manner to method A or B, was subsequently beached after

removing any macrophytes or debris. Macrophytes grew back in 2–4 weeks, and calibrations and surveys covered a negligible proportion of all habitats in the region. Rotenone, as derris powder steeped in 96% ethanol, was applied at 2 ppm in some calibrations following the 25-m seine haul (Appendix 1).

Habitats and taxa sampled.—Calibration sites were chosen to be representative of seasonal conditions that typified seinable floodplain habitats that were frequently included in surveys. They were performed during falling water levels in September and October, during rising levels in January on Marchantaria Island, and during rising levels in April and May at São José, Janauarí (Appendix 1). Water level movements are so gradual that floodplain conditions are effectively lacustrine (Figure 1), except during a short period of river invasion at maximum water stage through exposed areas that were not sampled at that time. Appendix 1 summarizes the quantities and size ranges (1.0–79.5 cm) of marked and unmarked fish from the 22 calibration experiments. A size range of 0.9–99.5 cm was caught in a 3-year survey comprising 600 seine samples.

Marchantaria Island is in the River Solimões-Amazonas and is completely influenced by its turbid waters. The fauna are dominated by Characoidei and Siluriformes. São José is near the extremity of turbid water influence, where the Amazon water is mixed with black waters from the Rio Negro but still has low clarity. This area contains more Cichlidae, although both areas show considerable overlap down to the species level.

Twenty-nine groups were constructed for exploratory analysis (Table 1). One group included the decapod, *Macrobrachium amazonicum*; therefore, the term 'fish' may include this species. These preliminary groups were selected according to their morphology, known ecology, and pertinent behavioral characteristics that could affect catchability. Much of the behavioral information was learned from fishers with 2–3 decades experience using seines and contrasting capture methods.

Analytical Framework

This section describes the estimation and validation of catchability. For a given species group and fish size, catchability q_s is given generically by

$$q_s = \frac{c}{v}, \qquad (1)$$

where c = number caught in the 25-m seine and

TABLE 1.—Species-groups considered with numbers encountered and length ranges (cm) of individuals.

Taxa	Initial species groups	Groups used in models[a]	Number of individuals caught	Length range (cm)
Tetragonopterinae	1	I	16,845	1.3–8.3
Brycon spp.	1	I	1,030	1.7–7.8
Curimatidae	2	I	2,805	1.7–17.0
Prochilodontidae	3	I	7,161	1.4–31.0
Serrasalmidae	4	I	1,303	1.4–32.5
Roeboides spp.	5	I	923	2.1–15.5
Triportheus spp.	6	I	715	1.9–21.5
Hemiodontidae	7	I	126	2.2–23.0
Anostomidae	8	I	96	2.8–30.0
Engraulidae	9	I	92	1.8–14.0
Cyprinodontidae	10	I	73	1.8–4.4
Microphylipnus sp. (Eleotridae)	10	I	5	1.9–2.3
Colomesus sp.	11	I	51	1.6–9.3
Cynodontidae	12	I	14	9.8–27.0
Osteoglossum sp.	12	I	4	10.0–35.0
Clupeidae	12	I	1	19.0–19.0
Chalceus sp.	12	I	1	3.2–3.2
Thorocharax sp.	12	I	1	4.9–4.9
Potamoraphis sp.	13	I	7	7.8–22.5
Boulengerella sp.	13	II	2	21.0–24.0
Geophagus and *Satanoperca* sp.	14	II	1,512	1.3–21.5
Acarichthys heckeli	15	II	1,105	1.8–16.5
Mesonauta insignis	16	II	467	1.3–11.5
Cichla spp.	17	II	98	3.3–38.5
Sciaenidae	18	II	49	1.2–12.5
Cichlidae not in groups 14–17	19	II	1,698	1.4–27.0
Macrobrachium (Decapoda)	20	II	5,105	1.6–8.7
Pimelodus blochi	21	III	741	5.2–21.0
Pimelodella and *Pimelodina* spp.	22	III	201	3.7–19.8
Pseudoplatystoma spp.	23	III	25	16.5–45.5
Hemisorubim platyrhynchus	23	III	6	12.0–38.5
Callichthyidae	24	III	540	1.4–20.5
Doradidae	25	III	118	3.5–44.5
Auchenipteridae	25	III	5	4.4–20.0
Loricariidae	26	III	152	2.2–38.0
Trichomycteridae	26	III	5	3.9–4.7
Hoplias malabaricus	27	III	76	1.0–39.0
Crenicichla spp.	28	III	38	3.3–30.5
Synbranchus marmoratus	28	III	25	7.4–79.5
Gymnotiformes	28	III	42	2.4–30.5
Potamotrygon sp.	29	III	5	15.0–55.0

[a] Generic descriptions are as follows: I, midwater–surface inhabitants with tendency to school in single- or multispecies groups; II, territorial or with tendency to seek physical cover; less frequent schooling behavior; III, demersal or eel-like fish associated with physical cover; less frequent schooling behavior.

v = number vulnerable in the area swept by the 25-m seine.

The number of fish originally vulnerable inside the block net, v_b, is estimated by adding the 25-m seine catch to the numbers caught by the block net, c_b, the latter corrected by the block net retention estimate, $\hat{q}_b$:

$$\hat{v}_b = c + \frac{c_b}{\hat{q}_b}. \tag{2}$$

A previously developed model (Bayley 1993) was used to estimate block net retention, q_b, from mark–recapture data defined by

$$\hat{q}_b = \text{(no. marked fish recaptured in block net)}$$

$$\div \text{ (no. marked fish remaining in block net}$$

$$\text{after 25-m net haul).} \tag{3}$$

The number of vulnerable fish in the area swept by the 25-m seine, v, is estimated by

Inputs	Quantity to be determined	Description
Unmarked fish captures: c in 25-m seine, c_b in block net. Block Net Retention (eq. (3)), $\hat{q}_b$	$\hat{v}_b = c + \dfrac{c_b}{\hat{q}_b}$	$\hat{v}_b$ = prediction of vulnerable fish abundance in block net
Area swept by the seine, A_s Area covered by block net, A_b	$\hat{v} = \dfrac{A_s}{A_b}\,\hat{v}_b$	$\hat{v}$ = prediction of vulnerable fish in the area swept by the seine
	$\hat{q} = \dfrac{c}{4\hat{v}}$	$\hat{q}$ = catchability based on estimated fish in an area that is a constant multiple (4) of the area swept by the seine (response in interval [0,1] used in statistical analysis, Appendix 3)
	$\hat{q}_s = 4\hat{q} = \dfrac{c}{\hat{v}}$	$\hat{q}_s$ = predicted catchability of seine based on area swept by the seine (variable reported in empirical results)
Retention efficiency of seine (see text under Simulation Approach), $\hat{q}_r$	$\hat{q}_e = \dfrac{\hat{q}_s}{\hat{q}_r}$	$\hat{q}_e$ = predicted encirclement efficiency of seine
Simulation model of seine encirclement, q_{esim}		comparison of simulated, $\hat{q}_{esim}$ and empirical, $\hat{q}_e$ encirclement efficiency estimates

FIGURE 2.—Steps and intermediate variables used in estimating and simulating catchability. Terms are defined in Table 2 and the text.

$$\hat{v} = \frac{A_s}{A_b}\hat{v}_b, \qquad (4)$$

where A_s and A_b are areas swept by the 25-m seine and block nets, respectively (see ratios in Appendix 1). Then catchability can be estimated as

$$\hat{q}_s = \frac{c}{\hat{v}}. \qquad (5)$$

Estimates of q_s were obtained based on a standardized area and quasi-likelihood model, as described in Appendix 3, with numerical examples given in Appendix 4. The complete set of equations, including those used in simulations, is il-

lustrated in Figure 2, and all symbols are described in Table 2.

Exploratory analyses of deviance (McCullagh and Nelder 1989) were performed to split data or coalesce categories and identify factors in the linear part of the model that would be most reliable in predicting catchability in addition to block net retention. This revealed that the categorical variables, method (A, B, C) (Appendix 1), taxa (3 major groups, Table 1), and individual length (first- or second-order polynomials) were strong predictors. These were retained in the order stated, whereas additional variables, including mean and maximum water depth, an index of vegetation den-

TABLE 2.—Symbols used. Numbers in parentheses correspond to numbered equations in text.

Terms	Description	Derivation
Generic		
Catchability (q_s) ($= q_e q_r$)	(Number caught)/(number initially vulnerable in area swept by 25-m seine)	
Encirclement (q_e)	(Number encircled by 25-m seine set)/(number initially vulnerable in area swept by 25-m seine)	
Retention (q_b, q_r)	(Number captured)/(remaining number in closed block net or seine before it is hauled)	
Specific		
c	Number caught in 25-m seine	Measured
c_b	Number caught in block net after hauling seine	Measured
q_b	Block net retention efficiency = number recaptured in block net/number remaining in block net after 25-m seine is hauled (3)	Estimated from mark–recapture data
v_b	Number vulnerable inside area swept by block net, $\hat{v}_b = c + (c_b/\hat{q}_b)$ (2)	Estimated
A_b (m^2)	Area swept by block net	Measured
A_s (m^2)	Area swept by 25-m seine	Measured
v	Number vulnerable inside area swept by 25-m seine (adjusted for varying ratio of areas of 25-m seine and block net), $\hat{v} = (A_s/A_b) \times \hat{v}_b$ (4)	Estimated
q_s	25-m seine efficiency = number caught in 25-m seine/estimated number vulnerable in area swept by 25-m seine, $\hat{q}_s = c/\hat{v}$ (5)	Estimated
q	25-m seine efficiency = number caught in 25-m seine/estimated number vulnerable in area four times that swept by 25-m seine (see Appendix 3)	Estimated
q_r	Retention efficiency of 25-m seine	Estimated
q_e	Encirclement efficiency of seine, $\hat{q}_e = \hat{q}_s/\hat{q}_r$	Estimated
q_{esim}	Simulated 25-m seine encirclement efficiency	Simulated

sity, turbidity (Secchi depth), density of vulnerable fish, and all first-order interactions, were tested in a reverse stepwise fashion. Correlated variables ($P < 0.05$) were tested alternately rather than jointly. Variables were retained at $P < 0.01$ based on change of deviance tests against χ^2. Models were also assessed, and continuous variables transformed, on the basis of visual assessment of standardized residual plots.

Empirical model validation.—Validation of empirical predictions was essential (1) because statistical analyses revealed departures from a binomial error distribution, (2) because a transformed response variable was used (Appendix 3), and (3) because of possible biases in the field procedure. Apart from inspection of model residuals as a function of predicted and explanatory variable values, the following two methods were used.

First, a cross-validation approach (Efron and Gong 1983) compared model predictions based on a random selection of 50% of the data, with the remaining, independent data point estimates excluded from the model. The unadjusted deviance residual (Pierce and Schafer 1986; McCullagh and Nelder 1989) was calculated for each independent data point, and each was compared with the empirical distribution of deviance residuals from the

model based on the other 50% of the data. Pierce and Schafer (1986) argued that deviance residuals should be much closer to a normal distribution than the standardized Pearson residuals. A departure from normality could not be detected from our deviance residuals. Therefore, the proportion of data points occurring within the 95% range based on 1.96 standard deviations predicted by the model are reported.

Second, the capture of marked fish by the 25-m seine provided direct estimates based on the smaller numbers and size ranges marked (Appendix 1). These fish had been distributed evenly inside the block net and were enclosed by the block net for a shorter period than the unmarked fish. On average, marked fish were in the block net 2.5–5 min before seining, which was one-third to one-half the time the unmarked fish were; therefore, less time was available for a possible change in spatial distribution due to the presence of the block net.

Simulation Approach

Catchability, the probability that a fish will be caught in the area swept by the 25-m seine, is the product of the probability of being encircled by the 25-m seine (encirclement efficiency, q_e = the complement of avoidance) and the probability of

being subsequently recovered from the net follow-
ing hauling (retention efficiency, q_r):

$$q_s = q_e q_r. \qquad (6)$$

q_e was simulated as q_{esim} for individual fish subject
to capture using method A within a 50-m block net
surrounding and concentric to the 25-m net. There-
fore, using a random distribution of initial location
in the block net, each fish had a probability of 0.25
of being in the area swept by the 25-m net.

Mean values of simulated q_{esim} were compared
with empirical estimates of 25-m seine encircle-
ment efficiency, $\hat{q}_e$. It could not be assumed that
25-m net retention efficiency was the same as that
for the 50-m block net. q_e was estimated graphi-
cally (Velleman 1988) by dividing the empirical
$\hat{q}_s$ predictions for each species group (Figure 7A)
by trial 25-m seine retention models of the func-
tional form derived for estimating block net re-
tention q_b (Figure 4) to predict q_e as a monoton-
ically decreasing function of fish length for each
species group. Resulting predictions of q_r were, as
expected for a smaller net, slightly higher than the
estimates for block net retention for each species
group.

The simulations, q_{esim}, incorporated four behav-
ioral variables: (1) fish swimming speed, (2) swim-
ming direction following each stimulus, (3) thresh-
old distance—how close to the source of distur-
bance (the moving boat and paddles) a fish must
be before altering its behavior (either to initiate
motion if stationary or to change direction if mov-
ing), and (4) appraisal time—how long a fish will
swim with no additional stimulus.

Direct experimental observation of individual
fish response to capture in turbid water at the scale
required was infeasible. However, realistic ranges
of values for simulation, summarized in the next
section, were constrained by accounting for the
following considerations.

Fish response to the fishing operation was ob-
served from a second stationary boat positioned
close to the seine net when taking several non-
calibration samples. The depth of observation was
limited by turbidity, as indicated by Secchi disk
readings (Appendix 1). Fish that could be observed
responded to the moving net using a 'kick-and-
glide' swimming mode, which is below the theo-
retical maximum relative speeds of 6–15 body
lengths per second (bl/s) of nonthunniform fishes
(Jobling 1995). Simulated swimming speeds were
allowed to vary between 1.3 and 10.7 bl/s.

The perception by fish of the boat, paddles, or
net may be visual or auditory and will affect
threshold distance and possibly directional re-
sponse. Whether the water is turbid because of
suspended clays ('white' water) or dissolved or-
ganic matter ('black' water), horizontal vision by
fish in Amazon waters is very limited due to light
scattering (Muntz 1982) and negligible compared
to average horizontal distances between fish and
boat.

Conversely, the known sensitivity of fish to
sound and/or hydrodynamic pressure, the previ-
ously described behavior of experienced fishers
when laying the seine, and direct observations of
responses of fish to deliberate pounding on the boat
all suggested potentially high auditory sensitivity.
However, directional response of fish to sound,
which the fishers believe emanates largely from
the paddling of the boat, is uncertain. The local-
ization and subsequent directional responses of
fish to a sound or pressure source are poorly known
and controversial, except for the recognized lo-
calization of intense signals in the acoustic near
field that were attributed to the lateral line system
(Fay 1988). However, following earlier evidence
of directional response by goldfish (Moulton and
Dixon 1967), cod have been determined to dis-
criminate sound sources down to 20° and 16° in
the horizontal and vertical planes, respectively
(references in Blaxter 1988; Fay 1988). In addi-
tion, sound source distance discrimination on the
scale of meters has been reported for cod (Schuijf
and Hawkins 1983).

However, it is still not clear how fish respond,
having received and discriminated a sound source.
Some fish may even be attracted to particular
sound sources (Blaxter 1988). Therefore, we have
simulated broad directional and nondirectional re-
sponses.

Threshold distance is therefore considered to de-
pend on response to sound detection. Whether
sound can be detected by all fish is questionable
given the shallow water and muddy substrates of
the sites sampled. Sound propagation in shallow
water over soft substrates cuts off at frequencies
less than 1,000 Hz at 1 m and less than 6,000 Hz
at 0.4 m deep, respectively (Rogers and Cox 1988).
These minimum frequencies represent upper hear-
ing ranges for non-Otophysan and Otophysan fish,
respectively, which are both commonly encoun-
tered. At least some fish will be at distances from
the sound source that exceed water depth, neces-
sitating interaction with the bottom and surface of
the sound waves, and most samples contain some
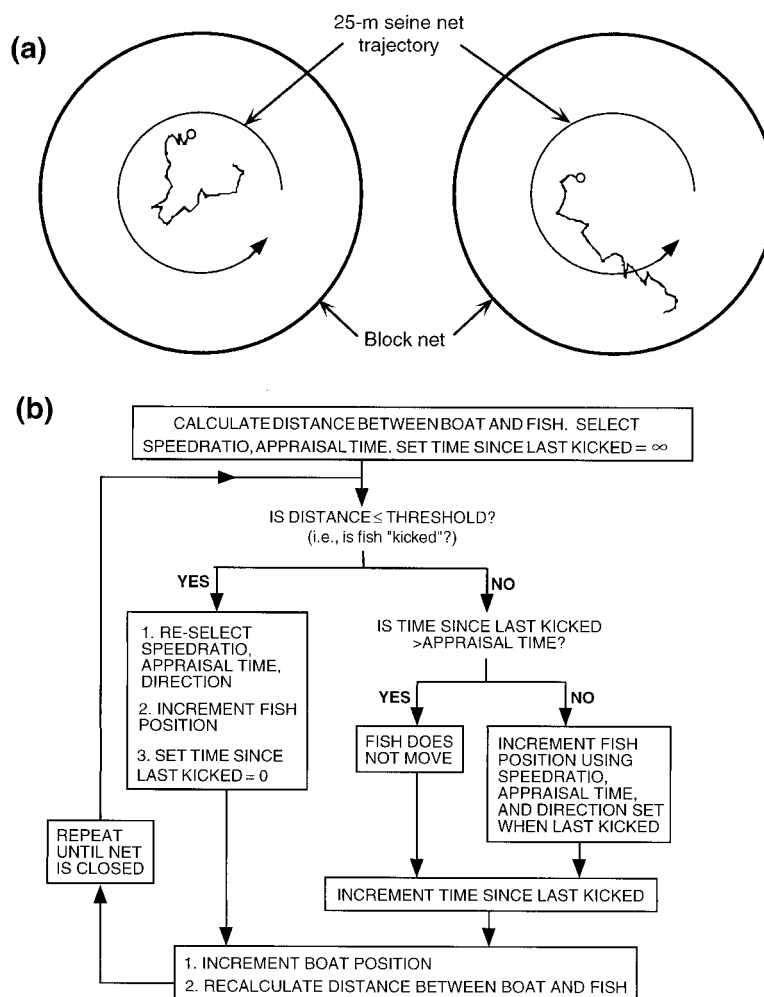areas shallower than the critical levels noted

FIGURE 3.—(a) Examples of two simulated capture attempts (chases). Open circle indicates starting location of fish. Mean threshold was 50%. Mean speedratio was equivalent to a swimming speed of 56 cm/s, (e.g., a 14-cm fish travelling at 4 body lengths/s). Mean appraisal time was 0.75 s. Example trajectories of a fish ultimately captured (left) and escaped (right) are shown. The boat laying the 25-m seine net started at the 3 o'clock position. (b) Logical structure of simulation model for the chase of a single fish. The 25-m seine was laid in 40 s, and the model's time step was 1 s. Threshold distance was held constant for each chase. Speedratio, appraisal time, and swimming direction were selected according to (partial) randomization, as discussed in the text.

above. This factor, plus the uncertainty about whether and how fish react to a received sound, caused us to simulate a wide range of threshold distances.

Appraisal time is difficult to predict. Observation of fish responding to a sound stimulus in shallow water indicated that accelerated swimming when startled generally ceased within about 0.5–1.0 s. Times ranging from 0.375 to 1.125 s and 1.0–3.0 s were simulated. When the appraisal time expired before the next stimulus, for example when it was less than the stimulation period or

when the fish was beyond the threshold, the fish was assumed to stop. Because 1 s is the mean period of the stimulation ('kick') rate of the paddles, the upper simulated range is only expected to be effective when the fish is beyond the current threshold distance.

Simulation Model Details

The model exploits the assumed radial symmetry of the seine, making the location of the boat simple to calculate, and is based on the assumption that (1) a fish can be represented as a point, even
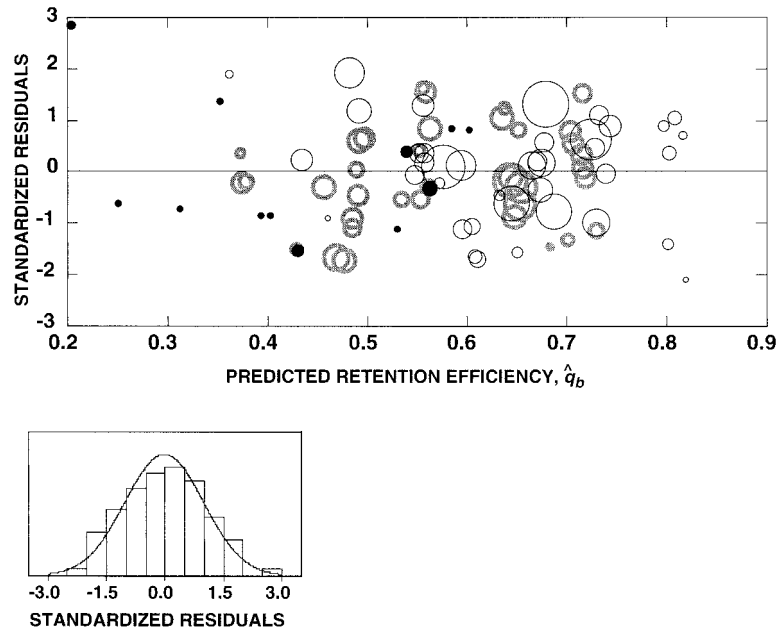
FIGURE 4.—Results of quasi-likelihood model fit to 50-m block net efficiency, $\hat{q}_b$, based on marked fish. Frequency plot of residuals (Pearson's are shown, deviance residuals were similar) in lower plot has normal distribution superimposed. The linear predictor, L, in the model was $2.34 - 1.35$(bottom fish) $- 0.62$(rotenone) $- 12.5$(fish length, mm)$^{-0.5}$, whose coefficients had respective standard errors of 0.39, 0.49, 0.19, and 2.8. Extra-binomial variance was 0.15. Block net efficiency was predicted via the logistic link by $1/[1 + \exp(-L)]$. Bottom fish (solid circles) comprised group III (Table 1) in nonrotenone calibrations. Rotenone (thick circles) comprised all species from calibrations using that treatment (Appendix 1). When these dummy variables are zero, the model predicts species groups I and II (open circles; Table 1) in nonrotenone calibrations. The symbol area is proportional to the number of vulnerable fish (marked and released).

though a 70-cm fish is 9% of the net's diameter; (2) disturbance from the boat may be considered as coming from a point source; (3) depth effects are negligible (see empirical results), making a two-dimensional approach appropriate; (4) fish do not school, so one fish can be modeled at a time.

A fish is assumed initially to be at rest at a randomly selected point inside the block net. The model simulates the fish's evasive behavior as the 25-m seine is laid (Figure 3a) using a logical process for each individual described in Figure 3b. The 25-m seine is laid in 40 s, with a paddle splash each second. The splash is the disturbance to which the fish is presumed to react and thus dictates the 1-s time step of the model. If a fish is within the threshold distance, it detects the presence of the boat and is said to be "kicked." In a standard run, this "chase" is repeated for each of 20,000 individual fish under the following ranges of the variables discussed above.

(1) Swimming speed is assigned values of 2, 4, and 8 bl/s ± 33% uniform distribution, resulting in ranges of 1.3–2.7, 2.7–4.3, and 4.3–

10.7 bl/s. These relative swimming speeds are applied to fish of six lengths ranging from 2.5 to 70 cm. Swimming speed is randomized at each kick within each chase. The boat is paddled at a speed of 0.625 m/s (= 25 m/40 s) to lay the net. The model uses the ratio of fish to boat speed, called "speedratio."

(2) Two swimming directional behaviors are used: directional response, in which the fish swims away at a random angle within ±90° of a straight line from the sound source, and nondirectional response, in which the fish swims in any direction with equal probability. Direction is randomized at each kick within each chase. Therefore, fish starting outside the area swept by the seine are sometimes encircled.

(3) Threshold distance is assigned values of 1 through 6 m ± 33% uniform distribution, resulting in ranges of 8–17, 17–33, 25–50, 33–67, 42–83, and 50–100% of the diameter (8 m) of the laid 25-m seine. Threshold is randomly varied among chases but not at each kick within a chase.
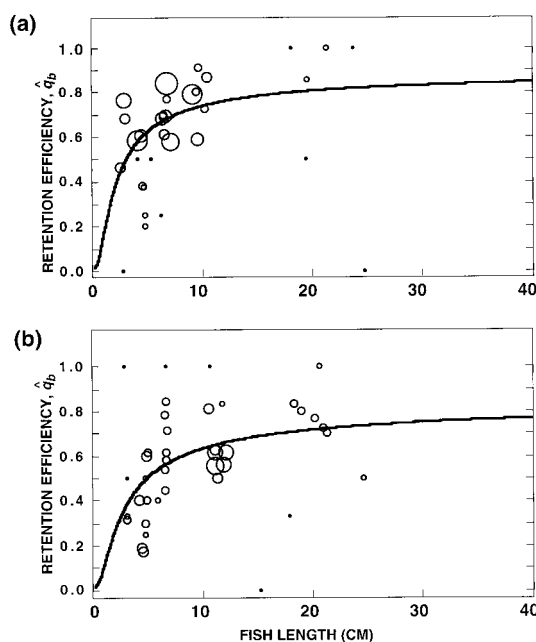
(4) Two appraisal times are used: 0.75 and 2.0 s

(a)

(b)

FISH LENGTH (CM)

FIGURE 5.—Examples of predicted values of model fit of block net retention, $\hat{q}_b$ (Equation 3) for **(a)** species groups I and II (Table 1) and **(b)** all species from calibrations in which rotenone was used (Appendix 1). Symbol area is proportional to number of vulnerable fish (marked and released).

$\pm$ 50% uniform distribution, resulting in ranges of 0.375–1.125 s and 1.0–3.0 s. Appraisal time is randomized at each kick.

In addition, there are assumed default behaviors when a fish encounters a net. If it hits the block net, it is stopped; hence, it is not encircled by the seine. If it encounters the unclosed seine, it is assumed to swim along it (when kicked and until the appraisal time has expired), leaving the net only if it reaches the end before closure. Fish were observed to be apparently unaffected when close to a stationary net in the absence of a sound source.

The program is written in TruBasic (available from R. Herendeen) and optionally displays the trajectory of each chase (Figure 3a). The result of each chase (where the fish started, whether it was encircled by the research net) is recorded.

Results

Block Net Retention

Independent samples estimating q_b were obtained by allocating fish into size-groups of 20–40, 40–80, 80–150, and 150+ mm. Standardized residuals from the quasi-likelihood analysis of the 70 q_b estimates appeared to be well behaved (Figure 4). The proportion of marked fish remaining in the block net that was subsequently retained by it, q_b, was dependent on whether rotenone was used and on two species groups (groups I and II combined and group III; Table 1) when rotenone was not used (Figure 4 caption). No taxa differences could be detected when rotenone was used. No first-order interactions were significant. Retention was not dependent on physical features measured. Retention increased rapidly with increasing fish size until approaching an asymptote (Figure 5), in a similar manner and magnitude to the function derived for recaptures from midwestern reservoirs following rotenone application (Bayley 1993). All fitted parameters (Figure 4 caption) were signifi-

TABLE 3.—Results of quasi-likelihood model fits to predict 25-m seine net efficiency, q_s, from unmarked fish, the predictive model recommended, and fish capture based on marked fish only. The three levels of SPGROUP are defined by species groups I through III (Table 1), respectively. The two levels of METHOD are defined by seining methods A and B combined and method C, respectively. Efficiency, q_s, is given by $4(1 + e^{-L})^{-2}$, where L is the linear predictor based on the coefficients below (see Appendix 4 for examples). Asterisks show significance levels (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$) of deviance change with removal of variable on a χ^2 distribution. Predictions are shown in Figures 6, 7, and 8.

Unmarked fish[a] (218 observations of 41,892 individuals)				Marked fish[b] (139 observations of 1,376 individuals)		
Coefficient	SE	Deviance change (df)	Covariate	Coefficient	SE	Deviance change (df)
2.2	0.74		1	4.70	1.96	
−0.422	0.130		SPGROUP(2)	−0.399	0.253	
−0.719	0.168	21.7 (2)****	SPGROUP(3)	−1.03	0.38	8.29 (2)*
−1.45	0.19	77 (1)****	METHOD(2)	−0.668	0.388	3.21 (1)
−0.524	0.163	11.3 (1)***	ln(Fish Length, mm)	−1.00	0.399	6.7 (1)**
−505	165	11.4 (1)***	(Fish Length, mm)$^{-2}$	−1,933	791	6.4 (1)*

[a] Extra-binomial variance = 0.12.
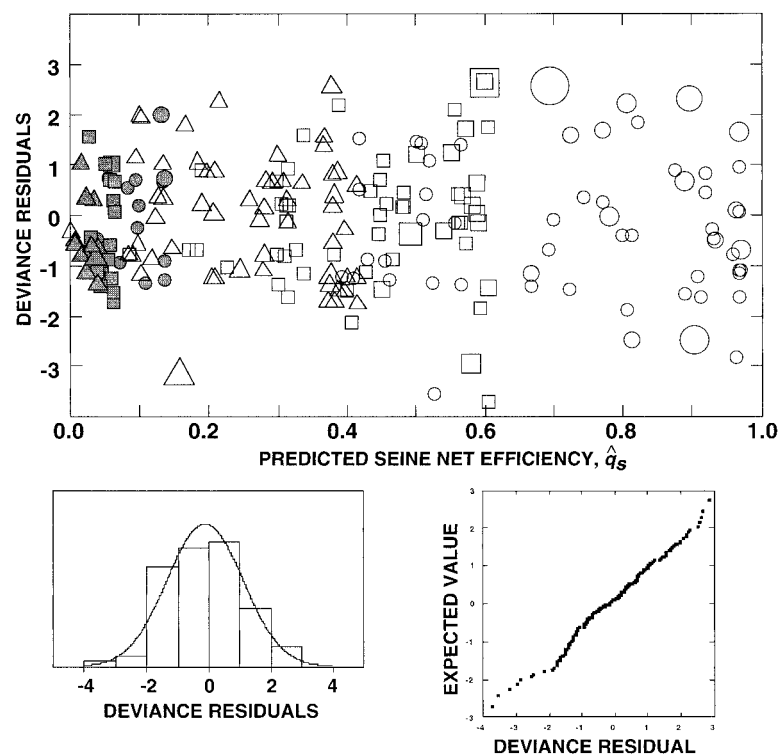[b] Extra-binomial variance = 0 (slight underdispersion).

FIGURE 6.—Deviance residuals of quasi-likelihood model fit to 25-m seine efficiency model for unmarked fish (Table 3). Species groups I, II, and III (Table 1) are denoted by circles, squares, and triangles, respectively. Seining methods A and B combined is represented by open symbols, and seining method C is represented by shaded symbols. Symbol area is proportional to number of vulnerable fish. Frequency plot of residuals has normal distribution superimposed (lower left) and a normal probability plot is shown at lower right.

cant at $P < 0.001$. For a given length, relative magnitudes of $\hat{q}_b$ were ranked as groups I, II (open water species) > rotenone (all species) > group III (bottom/eel-like species). Biological implications of these results are presented in the Discussion.

25-m Seine Efficiency

The same fish length-groups as in the block net retention analysis were used, yielding 218 observations. Fishing method, fish length, and species group (Appendix 1; Table 1) were highly significant explanatory variables (Table 3; Figure 6). Catchability was much lower using method C (hauling into canoe) than methods A or B, in which the lead line maintained contact with the bottom (Figure 7). There was no significant difference between methods A and B, which were subsequently pooled. No first-order interactions between method, species group, and fish length were detected; therefore, the more robust model that included all data points for all methods and calibrations (Table

3) was justified. The unimodal character of the fit (Figure 7) represented the product of the monotonically increasing retention efficiency, q_r (e.g., Figure 5), and monotonically decreasing encirclement efficiency, q_e (Figures 9 and 10). Two terms containing fish length (Table 3) were tuned through transformations to remove visible trends in the residuals when plotted with fish length and predicted efficiency (Figure 6). The ln(fish length) term dominated the relationship at fish lengths greater than 10 cm.

An exhaustive analysis of environmental factors (depth, turbidity, vegetation cover, substrate; see Appendix 1) did not indicate significant effects. Vulnerable numbers within taxa length-groups ranged from 1 to 2.3×10^4 individuals, but abundance within groups or totaled across taxa and/or length groups indicated no effect on catchability. When individual calibrations were statistically blocked, significant heterogeneity among calibrations was indicated, implying that unmeasured factors explain some of the variance.
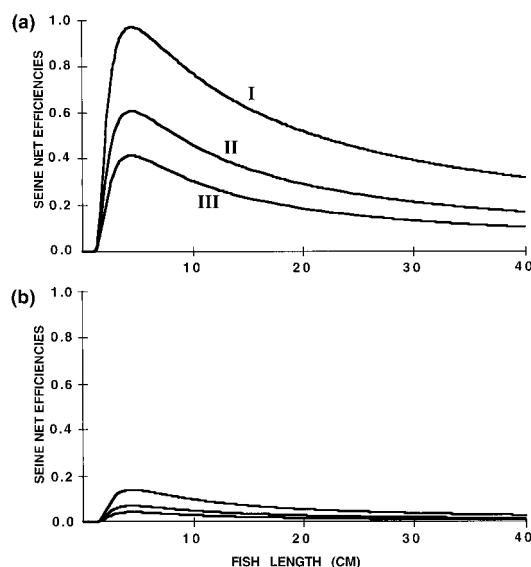
FIGURE 7.—Predicted values of model fit of seine net efficiency, $\hat{q}_s$, (Table 3, unmarked fish) for **(a)** seining methods A and B combined (both keeping lead line on the bottom while hauling) and **(b)** seining method C (lampara technique: hauled into boat in deeper water). Curves in **(a)** refer to species groups I, II, and III (Table 1); **(b)** shows those groups in the same order.

Some species jumped over the net on occasions, but only 15 individuals jumped out of the seine and one jumped out of the block net. These quantities were negligible compared with those lost invisibly through evasion or escapement.

The cross-validation method depended on deviance residuals being close to a normal distribution. Ratios of skewness and kurtosis to respective standard errors were only 0.20 and −0.14, respectively, and the linearity of the normal probability plot (Figure 6) suggested no serious departure. Deviance residuals from 96.4% of 110 randomly selected independent data points occurred within the 95% range from the model based on the other 108 points. Serial autocorrelation of residuals ordered by fish length, taxon, and calibration was not significant at $P = 0.05$. A model using the untransformed response was rejected because it exhibited highly skewed standardized Pearson and deviance residuals, with large departures from a mean of zero and a variance of one, and high extrabinomial variance (0.86).

Validation based on comparison of q_s based on marked fish caught by the 25-m seine was performed using the same length and species divisions used above. Several empty cells resulted from fewer individuals being available, and this analysis
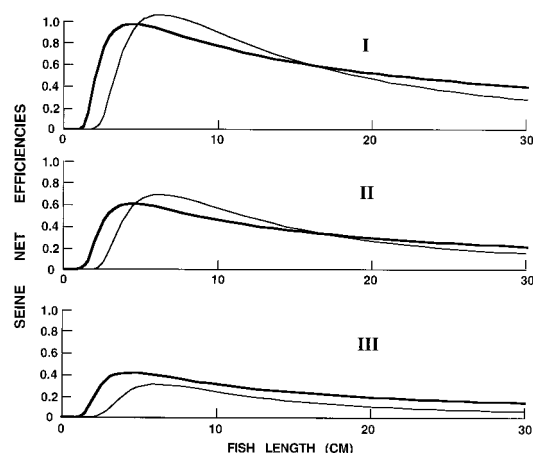

FIGURE 8.—Predicted values of model fits of 25-m seine efficiencies, $\hat{q}_s$, based on unmarked and marked fish (Table 3) for methods A and B combined for species groups I, II, and III. The thick line represents unmarked fish estimates; the thin line represents marked fish estimates.

was restricted to the subset of 17 calibrations in which marked fish were used (Appendix 1), but the results revealed similar coefficients (Table 3). Only the coefficient that distinguished methods did not have a significant deviance ($P = 0.07$). Marked fish were used in only two calibrations using method C. Plots of each species group using methods B or C (Figure 8) indicated reasonably close correspondence, except for smaller fish that were less well represented among the marked fish (Appendix 1). Catchability predictions for marked fish greater than 5-cm long were within the 95% maximum likelihood confidence intervals (Aitken et al. 1989) of the model for numbers of fish up to 500 (species group I), 400 (species group II), and 200 (species group III), where the greatest discrepancies occurred in each plot.

Simulations

Variances of simulation runs were virtually identical to theoretical binomial variances. Directional response, threshold, and swimming speed were the most influential variables affecting encirclement efficiency. The two appraisal time ranges generally produced similar results, with the longer one producing slightly lower efficiencies for moderate speeds. However, for swimming speeds greater than about 60 cm/s, the difference in mean q_{esim} exceeded 0.2 for thresholds greater than 50%. Although we argued previously that the shorter appraisal time range was more realistic, a longer
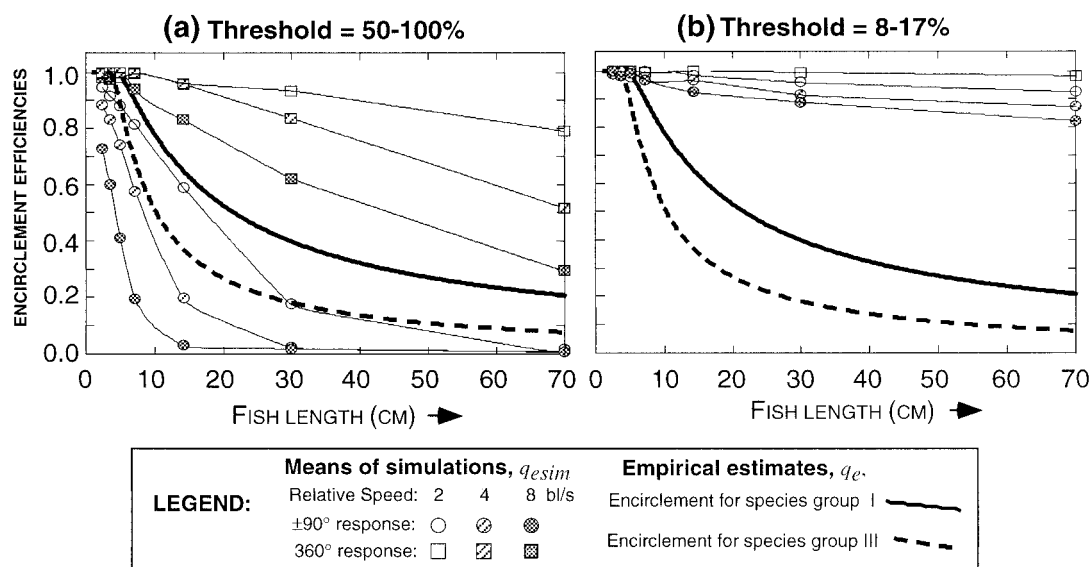
FIGURE 9.—Comparison of estimated ($\hat{q}_e$) and simulated (q_{esim}) 25-m seine encirclement efficiencies. Shown are encirclement efficiencies for extreme thresholds (50–100% 8–17% of 25-m seine diameter) in **(a)** and **(b),** respectively, for three relative speeds and directional ($\pm 90°$) versus nondirectional (360°) response. In **(b),** 360 responses for 2 body lengths/s shown, other speeds were similar. Empirical estimate for species group II is almost midway between those for groups I and III. Appraisal time = 0.75 s.

appraisal time would affect the following deductions for larger, faster fish.

Under extreme threshold ranges, mean encirclement efficiencies of nondirectional response simulation runs all exceeded mean empirical estimates of any of the three species groups (Figure 9). Subsequent comparisons were therefore limited to simulations of directional responses [Figures 9 (circles) and 10].

For fish larger than about 10 cm, species group I was fairly closely represented by a threshold range of 42–83% if the relative speed averaged 2 bl/s (Figure 10a), 33–67% for about 4 bl/s (Figure 10b), and marginally, 25–50% for about 8 bl/s (Figure 10c). In a parallel manner, fish greater than 10 cm long of the lowest catchability group (III) were roughly represented by a threshold range of 50–100% if the relative speed averaged 2 bl/s (Figure 9a), 42–83% for about 4 bl/s (Figure 10a), and 33–67% for about 8 bl/s (Figure 10b). For all fish 10 cm or less, empirical data indicated an approach to 100% encirclement, which was matched by low thresholds (<50%) and low relative speeds (<4 bl/s), implying that small fish only begin to sense and respond to the capture process at a closer distance and cannot swim so fast relative to their body length.

Obviously an inverse relationship exists be-

tween threshold and relative speed within certain limits for means of large numbers of individuals exceeding about 10 cm long. These outer limits are about 25–80% threshold for group I fish and about 33–100% threshold for group III fish (group II is intermediate), all within the full range of relative speeds simulated.

Discussion

The empirical results demonstrate that capture efficiency peaked at a fish length of 4–5 cm and then decreased with increasing length (Figure 7). It was also markedly affected at all sizes by two alternative modes of net operation and by broad species groups reflecting morphological differences and water column/substrate preferences. Effects of habitat could not be detected. However, although macrophytes and debris were the most variable features, their effect on efficiency was mitigated by their removal before hauling.

Biases resulting from the use of uncorrected catch data for estimating biomass or structure can be considerable. Applying the corrections developed here to the 3-year survey comprising 600 samples produced a sixfold difference in mean biomass based on efficiency-corrected data compared to the uncorrected catch data estimate. Nondimensional estimates were also affected: the effect of
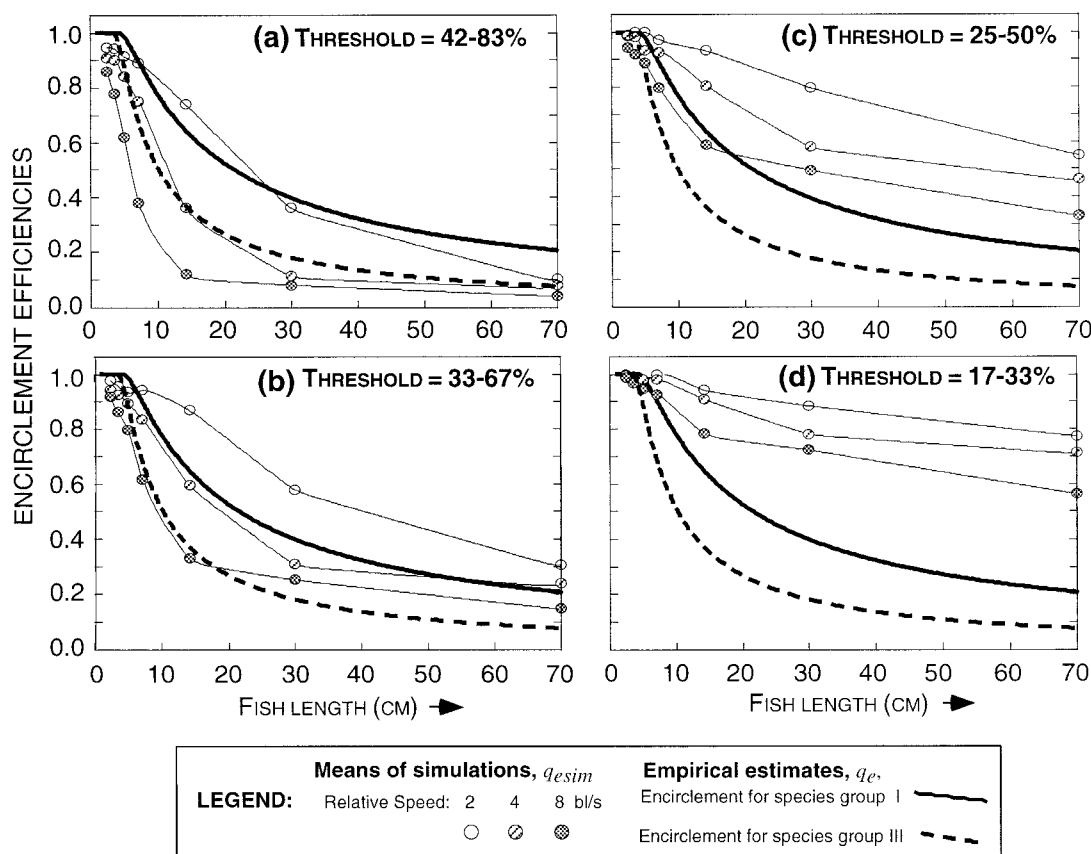
FIGURE 10.—Comparison of estimated ($\hat{q}_e$) and simulated (q_{esim}) 25-m seine encirclement efficiencies. Shown are encirclement efficiencies for thresholds of **(a)** 42–83%, **(b)** 33–67%, **(c)** 25–50% and **(d)** 17–33% of 25-m net diameter, with three relative speeds and directional response ($\pm90°$). Empirical estimate for species group II is almost midway between those for groups I and III. Appraisal time = 0.75 s.

fish size on catchability was apparent in estimating mean transfer efficiency (piscivore production/ prey production), in which piscivore lengths averaged four times those of their prey. Catchability-corrected analysis resulted in a transfer efficiency estimate of 0.20, whereas the estimated ratio based on uncorrected biomasses caught was only 0.09. If uncorrected, these biases would result in substantial underestimates of production and energy transfer or in other results that depend on abundance density or relative numbers at different fish sizes.

The simulations of net evasion indicated that a directional response to the disturbance was necessary to conform with empirical data, using a wide range of input values. The simulations also indicated that the drop in encirclement efficiency with increase in fish size could be described by

specific combinations of swimming speed and threshold distance. For a limited range of both variables, higher swimming speeds corresponded to lower thresholds for a wide range of fish sizes. Differences among species groups may result from different threshold values. Group II or III fish may not necessarily swim faster, but they may respond to the boat earlier. Studies to determine more precisely if preferred values of these components existed were beyond the resources of this project.

Viewing catchability as the product of the probability of encirclement and retention is useful in interpreting some published results. Useful information on retention efficiency has been obtained (Penczak and O'Hara 1983; Lyons 1986; Parsley et al. 1989; Pierce et al. 1990; Holland-Bartels and Dewey 1997) in experiments that ignored encirclement efficiency or presumed that it was unity,

although the potential for bias due to net avoidance was recognized (Lyons 1986; Parsley et al. 1989; Holland-Bartels and Dewey 1997). When fish size effects were detected, smaller fish tended to have lower retention (Pierce et al. 1990), as in this study. This is not unexpected, because smaller fish are expected to escape under the lead line after closure more easily than larger fish, with lower retention for bottom fish (group III), in addition to the selective effect of the mesh size itself.

The effects of various types of substrate on retention were categorized by Pierce et al. (1990) and Parsley et al. (1989) but are understandably difficult to quantify for predictive purposes and may be sensitive to behavioral characteristics of different species (Holland-Bartels and Dewey 1997). We recognize that removal of macrophytes in high-latitude systems that have limited standing crops and production may not be advisable for intensive sampling programs. Also, cobble/boulder substrates can present greater retention problems than macrophyte beds, and alternative methods, such as electrofishing, may be more appropriate. In environments where obstacles can be removed (and replaced when appropriate), the benefits of higher and more robust predictions can be worth the extra labor.

A much longer seine can sometimes be quickly lifted over occasional, isolated snags with low risk of escapement, but the association between length of seine and probability of encountering snags is self-evident. In our situation, a relatively short seine optimized the trade-off between retention and encirclement, as well as providing a quadrat size more appropriate for the spatial distribution of habitat. Increased drag due to clogging and snag encounter rate obviated a seine longer than 25 m. Conversely, the seine calibrated here would not be effective in clear, open water because encirclement efficiency would be reduced by large thresholds.

Other studies calibrate a method that itself restricts the degree to which fish can evade the net before closure, such as seining inside a blocked enclosure (Weinstein and Davis 1980; Holland-Bartels and Dewey 1997) or in a blocked channel (Wiley and Tsai 1983; Allen et al. 1992; Bayley and Dowling 1993). Where size effects were analyzed in several length-groups, lower catchabilities were detected for smaller (due to lower retention) and larger (due to avoidance) fish (Allen et al. 1992; Bayley and Dowling 1993) when avoidance was not prevented, as in this study. Obviously when blocking is part of the standard procedure, the blocking process should not promote

evasion. This is often achieved by rapid blocking across a distance that is small compared with the length or area of the resulting enclosure. Remote, simultaneous release of all parts of a block net from the surface minimizes this bias in open waters (Kapetsky 1980).

Evasion can be expected to be important when seining in an unrestricted area (Threinen 1956; Kjelson and Colby 1976; this study), making knowledge of size selectivity more critical. Threinen (1956) reported catchability by numbers of fish as 0.33–0.88 (median 0.47) and by biomass as 0.11–0.54 (median 0.22) for the same population of largemouth bass, indicating lower catchability for larger fish, as in this study.

There is a need for more studies to account for the effect of fish size as a continuous variable (Kjelson and Colby 1976), as well as a need to apply statistical methods that permit the inclusion and appropriate weighting of observations based on varying numbers of fish, for which one approach is outlined here. Such studies will need to budget for sufficient numbers of calibrations to unravel the potential confounding of size, species, and physical effects, especially when small numbers of fish are encountered per haul.

The magnitude and type of area in which the vulnerable population is estimated for calibration influences efficiency prediction. Calibration can be achieved by relating (1) single samples to density of fish retained within small enclosures, as in this study, or (2) aggregated catches from several samples to density estimated for each of several water bodies (Threinen 1956). Applying catchabilities from (2) to other environments depends on the prediction of an average catchability, which can be biased due to differences in habitat types among environments that affect efficiencies and/or gear operation. In addition, estimation of vulnerable populations in large areas is usually less precise. Therefore, an important requirement of calibration is to create an enclosure that is small enough to minimize these problems but not so small as to affect normal gear avoidance, affect the fish distribution due to the enclosure, or limit the desired size or species ranges of fish that can be enclosed.

Many published reports depend on multiple removal or uncalibrated higher efficiency methods, such as rotenone, to estimate the vulnerable population. Underestimation of population size by overestimating capture efficiencies has been found to occur using multiple removal (Mahon 1980; Rodgers et al. 1992) and uncorrected rotenone methods (Henley 1967; Axon et al. 1979; Bayley

and Austen 1990). Carefully conducted mark and recapture experiments are most likely to minimize this bias, given assumptions of similar catchability of unmarked and marked fish during calibration.

Water depth is expected to have an effect on efficiency. The method we employed was changed according to water depth, with method C producing strikingly lower catchabilities (Figure 7). Such low values must be influenced by the lower retention expected when the 25-m net leadline is lifted into the boat, but an additional effect of deeper water resulting in increased avoidance is plausible. Within methods, a depth effect was not detected, probably because fishing was confined within a maximum depth less than about half the hung depth of the net. However, lower catchabilities of groups II and III may be partly due to their preference for deeper water. It is also conceivable that low dissolved oxygen (DO) associated with deeper water or the bottom (Schmidt 1973; Junk et al. 1983) may limit escape speeds. Capture efficiency of the beach seining procedure, method B, was indistinguishable from method C. Although maximum depths associated with method B tended to be greater than in method C, avoidance may have been compensated in B because 24% of the enclosure perimeter is the shoreline.

Emergent vegetation, in the form of true floating or rooted types or partially decomposed clumps at or below the surface, was always removed following closure. However, vegetation could still affect encirclement efficiency. Despite wide variation in the vegetation index (Appendix 1), which was correlated with the proportion of surface coverage (range 0–30%), no effect on catchability could be detected. It was evident that many fish were associated with vegetation, especially along the edges of surface mats or meadows. However, daytime DO in vegetation is often 0–0.5 mg/L and H_2S is often present (Junk et al. 1983) due to decomposition and reduced circulation; therefore. its value as a refuge may be compromised for most fish species. Conversely, some Gymnotiform species (W. Crampton, University of Oxford, personal communication) and *Synbranchus marmoratus* that breathe atmospheric oxygen are frequently found in thicker vegetation. Our predictions may underestimate the catchability of such species when they are confined to floating mats. Under extreme cases, low DO can extend to areas of open water, when aquatic surface respiration by slow-moving fish can be observed. Encirclement and retention efficiencies will consequently be much higher than model predictions.

Predictions based on simulations will not yet substitute for good empirical data, given the paucity of data on the responses of fish to physical stimuli resulting from operations of a given method in a given physical environment and the effect of retention efficiency that is difficult to simulate. However, the scalability of the simulation model might be useful in predicting changes in efficiency in the same environment if, for example, the net length was changed. Prediction would be possible at different net scales if calibrations for longer nets validated the expected higher capture efficiencies of large fish, given similar turbidities and sound environments. Conversely, when a net has to be shortened to fish between snags, the expected lower efficiencies could be predicted.

In view of the complex individual and group behaviors expected among different taxa and fish sizes, obtaining a generalized but useful theoretical model for catchability will need more empirical data. Producing correctly bounded models with well-behaved residuals and acceptable validations, even if it means a combination of a generalized linear model and a variable transformation, is justified in the short term. In the longer term, it is hoped that improved error distribution specifications will produce robust catchability models that can summarize fish response to capture across sets of related capture methods. Extended by appropriate simulation, this process should mitigate the investment needed for empirical determinations in all methods and habitats of interest. The abundance of new approaches to tackling overdispersion in the recent statistical literature suggests that availability of analytical tools will not limit this process. Also, theoretical guidance for application of catchability information to different sampling designs is available (Thompson and Seber 1994).

In our study, it was not possible to directly relate empirically derived coefficients to any derived from models based on the simulations. Although we kept the simulation process as simple as possible, nonlinear effects were inevitable. However, for given mean input values, the error distribution was very close to the binomial. Arguments for sources of extra-binomial variation are given elsewhere (Bayley 1993). The overdispersion estimated for the empirical data are probably partly a result of groups of individuals not responding individually, such as those trying to escape as schools.

Conversely, variance among samples due to spatial heterogeneity on the larger scales associated

with a survey is expected to be greater. For larger fish, the effect of sparse distributions is compounded by the coefficient of variation of efficiency that increases with decreasing efficiency. Numerous samples are needed to obtain acceptable density estimates for larger fish. For example, in the Amazon survey mentioned previously, efficiency-corrected data produced coefficients of variation of mean biomass density of 32%, 40%, and 95% for fish 12–24, 24–48, and 48–96 cm, respectively, for all species combined. Although the low-efficiency method C had to be used in about a third of these samples and reduction of this variation through temporal and spatial stratification has not been investigated, there is a fundamental limitation on precision estimates due to the small area of the seine relative to the sparse distribution of larger fish. Methods that cover large areas combined with better catchabilities for larger fish, such as boat electrofishing or trawling, become more attractive in appropriate physical conditions. Commercial fishers use longer beach seine and lampara nets of larger mesh sizes in the Amazon but use them in open water or productive migration zones that have been cleared of vegetation at low water.

In conclusion, despite high species diversity and increasing scarcity of fish numbers with increasing size, simulations of encirclement for given speed and threshold conditions within expected physical and behavioral limits were consistent with empirical estimates. Given large numbers of noncalibration samples and an appropriate design, applying this calibration approach provides accurate estimates of abundance and related population measures and is far more cost effective than attempting population estimates on a sample-by-sample basis.

Acknowledgments

References

Aitken, M., D. Anderson, B. Francis, and J. Hinde. 1989. Statistical modelling in GLIM. Clarendon Press, Oxford, UK.

Allen, D. M., S. K. Service, and M. V. Ogburn-Matthews. 1992. Factors influencing the collection efficiency of estuarine fishes. Transactions of the American Fisheries Society 121:234–244.

Axon, J. R., L. Hart, and V. Nash. 1979. Recovery of tagged fish during the Crooked Creek Bay rotenone study of Barkely Lake, Kentucky. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 33(1980):680–687.

Bayley, P. B. 1993. Quasi-likelihood estimation of marked fish recapture. Canadian Journal of Fisheries and Aquatic Sciences 50:2077–2085.

Bayley, P. B., and D. J. Austen. 1990. Modeling the sampling efficiency of rotenone in impoundments and ponds. North American Journal of Fisheries Management 10:202–208.

Bayley, P. B., and D. C. Dowling. 1993. The effect of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. Polish Archives in Hydrobiology 40:5–14.

Blancheteau, M. L., P. Mousset, and G. Vibert. 1961. Etude neurophysiologique de la pêche électrique-Courant continu. Bulletin du Centre d'Etudes et de Recherches Scientifiques Biarritz 3:275–382.

Blaxter, J. H. S. 1988. Sensory performance, behavior, and ecology of fish. Pages 203–232 in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga, editors. Sensory biology of aquatic animals. Springer-Verlag, New York.

Efron, B., and G. Gong. 1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. American Statistician 37:36–48.

Fay, R. R. 1988. Peripheral adaptations for spatial hearing in fish. Pages 711–731 in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga, editors. Sensory biology of aquatic animals. Springer-Verlag, New York.

Fittkau, E. J., V. Irmler, W. J. Junk, F. Reiss, and G. W. Schmidt. 1975. Productivity, biomass, and population dynamics in Amazonian water bodies. Pages 289–311 in Z. B. Golley and E. Medina, editors. Tropical ecological systems. Springer-Verlag, New York.

Fredin, R. A. 1950. Fish population estimates in small ponds using the marking and recovery technique. Iowa State Journal of Science 24:363–384.

Hartley, W. G. 1967. Electronarcosis of fish for handling. Pages 251–255 in R. Vibert, editor. Fishing with electricity. Fishing News Books, Oxford, UK.

Hayes, M. L. 1983. Active fish capture methods. Pages 123–145 in L. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Henley, J. P. 1967. Evaluation of rotenone sampling with SCUBA gear. Proceedings of the Annual Confer-

ence Southeastern Association of Fish and Wildlife Agencies 20(1966):439–446.

Holland-Bartels, L. E., and M. R. Dewey. 1997. The influence of seine capture efficiency on fish abundance estimates in the upper Mississippi River. Journal of Freshwater Ecology 12:101–111.

Jobling, M. 1995. Environmental biology of fishes. Fish and fisheries series 16. Chapman and Hall, London.

Junk, W. J. 1973. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, part 2: the aquatic fauna in the root zone of floating vegetation. Amazoniana 4:9–102.

Junk, W. J., G. M. Soares, and F. M. Carvalho. 1983. Distribution of fish species in a lake of the Amazon river floodplain near Manaus (Lago Camaleão), with special reference to extreme oxygen conditions. Amazoniana 7:397–431.

Kapetsky, J. M. 1980. Addendum to chapter 8 (chemical methods). Pages 105–113 in T. Backiel and R. L. Welcomme, editors. Guidelines for sampling fish in inland waters. FAO (Food and Agriculture Organization of the United Nations), EIFAC Technical Paper 33, Rome.

Kjelson, M. A., and D. R. Colby. 1976. The evaluation and use of gear efficiencies in the estimation of estuarine fish abundance. Pages 416–424 in M. Wiley, editor. Estuarine processes, volume 2. Academic Press, New York.

Lamarque, P. 1963. Les réactions du poisson dans la pêche électrique et leur explication neurophysiologique. Science Progrès La Nature 3336:137–148.

Lyons, J. 1986. Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. North American Journal of Fishing Management 6:288–289.

Mahon, R. 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. Environmental Biology of Fishes 5:343–360.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London.

Moulton, J. M., and R. Dixon. 1967. Directional hearing in fishes. Pages 187–232 in W. N. Tavolga, editor. Marine bio-acoustics. Pergamon, Oxford, UK.

Muntz, W. R. A. 1982. Visual adaptations to different light environments in Amazonian fishes. Revue Canadienne de Biologie Experimentale 41:35–46.

Parsley, M. J., D. E. Palmer, and R. W. Burkhardt. 1989.

Variation in capture efficiency of a beach seine for small fishes. North American Journal of Fisheries Management 9:239–244.

Penczak, T., and K. O'Hara. 1983. Catch-effort efficiency using three small seine nets. Fisheries Management 14:83–92.

Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. Canadian Journal of Fisheries and Aquatic Sciences 47:1004–1010.

Pierce, D. A., and D. W. Schafer. 1986. Residuals in generalized linear models. Journal of the American Statistical Association 81:977–986.

Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12:79–86.

Rogers, P. H., and M. Cox. 1988. Underwater sound as a biological stimulus. Pages 131–149 in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga, editors. Sensory biology of aquatic animals. Springer-Verlag, New York.

Schmidt, G. W. 1973. Primary production of phytoplankton in the three types of Amazonian waters. II. The limnology of a tropical flood-plain lake in Central Amazônia (Lago do Castanho). Amazoniana 4:139–203.

Schuijf, A., and A. D. Hawkins. 1983. Acoustic distance discrimination by the cod. Nature (London) 302:143–144.

Thompson, S. K., and G. A. F. Seber. 1994. Detectability in conventional and adaptive sampling. Biometrics 50:712–724.

Threinen, C. W. 1956. The success of a seine in the sampling of a largemouth bass population. Progressive Fish-Culturist 18:81–87.

Velleman, P. F. 1988. Data desk version 5.0. Data Description, Inc., Ithaca, New York.

Weinstein, M. P., and R. W. Davis. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. Estuaries 3:98–105.

Wiley, M. L., and C.-F. Tsai. 1983. The relative efficiencies of electrofishing vs. seines in Piedmont streams of Maryland. North American Journal of Fisheries Management 3:243–253.

Williams, D. A. 1982. Extra-binomial variation in logistic linear models. Applied Statistics 31:144–148. (Royal Statistical Society, London.)

Appendix follows

Appendix 1: Habitat and Catch Data

TABLE A1.1.—Habitat and operational features and catch summaries of the 22 calibrations.

Method	Sample[a]	Rotenone use	Area ratio[b]	Depth (cm) Secchi disk	Depth (cm) Minimum	Depth (cm) Maximum	Vegetation[c]	Substrate[d]	Unmarked fish caught[e]
A	01	Yes	2.78	13	65	70	4	2	305
A	03	Yes	3.45	15	50	60	0	1	716
A	04	Yes	2.27	20	65	90	0	1	13,499
A	05	Yes	2.63	20	85	95	0	1	5,880
A	06	Yes	2.63	17	70	100	0	1	521
A	09	No	3.45	100	80	80	12	3	527
A	10	No	3.45	60	80	80	64	3	1,166
A	11	Yes	3.45	70	75	80	80	3	5,104
A	12	No	3.85	50	70	75	60	3	4,682
A	18	No	2.22	100	30	150	28	3	826
A	19	No	2.17	140	30	130	8	3	304
B	07	Yes	2.22	20	0	90	0	2	1,895
B	13	No	2.22	100	0	80	0	3	318
B	14	No	2.22	100	0	140	8	3	561
B	15	No	2.22	120	0	160	36	3	224
B	16	No	2.22	150	0	135	44	3	1,403
B	17	No	2.22	140	0	130	32	3	2,107
C	02	Yes	2.63	13	60	60	0	2	1,152
C	08	Yes	2.63	20	80	160	0	2	167
C	20	No	2.13	140	70	150	4	3	325
C	21	No	2.04	140	80	280	8	3	108
C	22	No	2.50	140	60	230	8	3	102
	All								41,892

[a] Samples 12 or less were located at Marchantaria Island, the remainder at Janauarí.
[b] Ratio of area covered by block net, A_b, to that swept by 25-m net, A_s.
[c] Index of total quantity of macrophytes and debris in seine net, measured as the number of person-minutes required to clear it (referred to as ''vegetation'' or ''cover'' in text).
[d] Bottom hardness assessed subjectively from 1 = soft to 3 = hard.
[e] Fish includes the decapod *Macrobrachium amazonicum.*

Appendix 2. Marking and Handling Fish

A galvano-narcotic trough, using a continuous DC (≤48 V) to hold a fish pointed toward the anode in a state of galvano-narcosis (Blancheteau et al. 1961; Lamarque 1963; Hartley 1967), minimized handling during marking and measuring with no discernible after-effect during the 60–90 min of the experiment. The water level in the trough was adjusted so that the fish lay on one side, facilitating photography for subsequent identification and measurement from a 1-cm grid on the bottom. A small correction to these measurements was found by calibration. Fish length was measured to the end of the median caudal fin rays: 'fork length' for most species. The cathode was moved toward the anode to increase the voltage gradient for fish less than about 50 mm long. The trough worked well with conductivities down to 50 μS/cm (20°C), below which a minimal quantity of salt was added.

Fish concentrated by the seine net were transferred to the trough and subsequently to the holding bins using containers to avoid ever being removed from the water. An oblique clip removed a third of the upper caudal fin lobe. These clips were distinct from piranha bites, which often remove a greater portion of the caudal fin. Fish down to 20 mm long were marked and released with 100% survival, except Engraulidae and Clupeidae, which suffered trauma from seining even though they were never removed from the water.

TABLE A1.1.—Extended.

Method	Unmarked fish			Marked fish released	Marked fish			
	Number caught in seine	Minimum fork length (cm)	Maximum fork length (cm)		Number caught in seine	Number caught in block net	Minimum fork length (cm)	Maximum fork length (cm)
A	41	2.0	34.5	91	20	35	2.6	38.5
A	258	1.2	25.5	98	24	40	3.5	34.0
A	9,695	1.3	49.0	144	63	47	2.9	31.0
A	4,040	1.0	42.5	69	11	42	3.4	34.5
A	217	1.4	48.5	71	26	25	3.5	23.0
A	117	1.4	41.0	52	3	34	2.4	24.5
A	542	1.4	11.0					
A	1,648	1.4	48.5	39	3	11	2.6	15.0
A	2,362	1.5	51.0	106	21	50	2.0	7.8
A	450	1.5	79.5	168	27	112	3.4	12.0
A	108	1.6	16.5					
B	246	1.3	19.5	40	7	27	4.3	32.5
B	79	1.5	33.0	104	11	57	2.0	34.5
B	305	1.3	21.5	45	7	24	5.1	39.0
B	59	1.4	15.5	94	12	46	2.7	35.5
B	977	1.4	34.5	82	26	39	3.5	29.0
B	851	1.3	64.5	47	15	24	2.5	32.0
C	216	1.6	22.5	74	12	39	2.8	27.0
C	11	1.8	5.5	52	6	25	3.6	29.5
C	41	1.8	20.0					
C	2	1.6	44.5					
C	3	1.9	14.5					
	22,268	1.0	79.5	1,376	294	677	2.0	39.0

Appendix 3. Empirical Model of Catchability

Conceptually, catchability should be represented as a fraction of fish caught ($0 < \hat{q}_s < 1$), which also represents a bounded response that can be analyzed statistically using binomial-related models. However, as formulated in Equation 5, not all empirical $\hat{q}_s$ estimates will conform: $\hat{q}_s$ can exceed one for some size–taxa combinations because the chance distribution of small numbers of fish or fish schools sometimes results in proportionately more fish being inside the area swept by the seine net. Catchability based on the numbers originally inside the block net (catchability = c/v_b) will provide estimates less than one. However, the ratio of block net enclosed area (A_b) to seine swept area (A_s) is not constant because of different methods and departures from geometrically perfect configurations in the field (Appendix 1). Therefore, for a given individual probability of capture, as A_b/A_s increased, catchability thus estimated would become negatively biased. We corrected this bias by estimating the vulnerable fish in an area that was a standard multiple of the area swept by the seine, A_s. A multiple of four exceeded all A_b/A_s values; therefore, this standard assured that all estimates of the response variable ($\hat{q} = \hat{q}_s/4$) remained in the range [0, 1]. Any multiple greater than A_b/A_s could have been used. Most empirical $\hat{q}$ values are less than 0.25, but occasionally some species size-groups of few individuals are captured by the seine net entirely by chance, producing larger, but valid estimates of $\hat{q}$ ($= A_b/4A_s$).

For consistency of presentation, all catchability results are reported that correspond to the more intuitive $\hat{q}_s$ in Equations 4 and 5 by multiplying model predictions of q, based on $\hat{q}$, by four. Note that a species responding to the seine by herding (more fish entering than exiting the swept area) could result in a model prediction of $\hat{q}_s > 1$, which would be a correct representation of the process. The full model used in the statistical analysis is described as follows.

Although q is a fraction, preliminary logistic-linear analyses based on maximum

likelihood assumption of a binomial error distribution indicated considerable additional error variance (overdispersion). The binomial model requires, unrealistically, that the errors are independently and identically distributed among all individual fish (Bayley 1993). Also, the binomial index, $\hat{v}$, is an estimate based partly on $\hat{q}_b$ (Equation 4) rather than being directly enumerated. In addition, in the logistic-linear version, the variation of mean catchability must be completely described by a linear function of the type

$$\eta = \sum \beta_j x_j = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots \beta_k x_k = \beta' \underline{x}, \qquad (A3.1)$$

in which the linear predictor, η, is determined by k explanatory variables (factors and/or covariates), x_j (x_0 is unity), and unknown parameters, β_j. Equation A3.1 is related to the response by the following logistic ''link'' function:

$$g(q) = \eta = \log_e(q/(1 - q)) = \text{logit}(q) \qquad (A3.2)$$

Because of the expected and observed departures from the binomial variance model, a fitted extra-binomial variance parameter added to the linear part of the model (Equation A3.1) using a quasi-likelihood approach based on Williams' model III (Williams 1982; Bayley 1993) produced the better results, as subsequently confirmed by residual inspection and validation. Using Equation A3.1, the binomial variance of the response, as numbers of fish caught, is consequently increased by a factor $\{1 + \sigma^2(m - 1)q(1 - q)\}$, where m is the number of fish vulnerable (binomial index). This is also the variance function used in determining the block net retention model.

Other link functions (probit, complementary log-log) produced very similar results. However, q deviance residuals were always strongly positively skewed and large extra-binomial variance estimates ($\sigma^2 > 0.8$) resulted. Williams' (1982) model II also produced similar results. Although Pierce and Schafer (1986) argued that deviance residuals should be closer to normality than alternatives, that distribution is not a required assumption. However, considering the departures from the binomial model and our derived binomial index values (Equation 2), our overriding concern was to produce a model that could be reliably validated (see Empirical Model Validation). A square root transformation of the response variable, q, maintained the correctly bounded model structure and produced similar coefficient estimates and predictions but produced a residual distribution close to normal and a low extra-binomial variance. The resulting transformed quasi-likelihood logistic link model used for catchability q ($= q_s/4$) can be summarized as

$$\sqrt{q} = (1 + \exp(-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k + \epsilon)))^{-1}, \qquad (A3.3)$$

where ϵ is a random error whose square was estimated as the extra-binomial variance, σ^2, using an iterative macro that interfaced with the GLIM4 statistical package (Bayley 1993). Other packages with adequate interfacing, such as S-plus, could be used. In the GLIM4 procedure, square roots of the numbers of fish caught, c, in each taxa length-group and of the corresponding estimates of vulnerable fish, v, were input as response and binomial index, respectively, where $\sqrt{q} = \sqrt{c}/\sqrt{v}$. Numerical examples of the final model are shown in Appendix 4.

Appendix 4. Numerical Examples

Example 1: Consider a sample of species group III [SPGROUP(3)] fish from the 80–150-mm length-group of mean length 100 mm encountered in calibration No. 11 that used method A (Appendix 1). In this group, the number of unmarked fish captured by the 25-m seine, $c = 3$; by the block net, $c_b = 12$; and the ratio of 25-m seine and block net areas, $A_s/A_b = 0.29$. From the equation coefficients in the Figure 4 caption, block net retention efficiency, q_b, based on rotenone is estimated as $q_b = (1 + e^{-L})^{-1}$, where

L is the linear predictor [$= 2.34 - 1.35 \cdot 0 - 0.62 \cdot 1 - 12.5(100)^{-0.5} = 0.470$]. Therefore, $q_b = 0.6154$.

From Equation 4, estimated vulnerable fish, $\hat{v} = 0.29(3 + 12/0.6154) = 6.52$, and from Equation 5, the sample catchability estimate $q_s = 3/6.52 = 0.46$.

The model prediction of seine catchability uses the linear predictor derived from the coefficients for unmarked fish (Table 3), $L = 2.22 - 0.422 \cdot 0 - 0.719 \cdot 1 - 1.45 \cdot 0 - 0.524 \ln(100) - 505 \cdot 100^2 = -0.9626$, whence $\hat{q}_s = 4(1 + e^{-L})^{-2} = 0.31$.

Example 2: To convert catch to fish density, we require the area swept by the seine. Consider the catch of 10 specimens of a group I fish at length 150 mm using method A. The model (Table 3, unmarked fish) predicts $\hat{q}_s = 0.624$. If the area swept by the 25-m seine is 50 m^2, then estimated density $= 10/(50 \cdot 0.624) = 0.32$ individuals/m^2.